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The Effect of Light Intensity on Sockeye Salmon Fry Migratory Behavior and Predation by Cottids in the Cedar River, Washington

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Abstract.—We examined the relationship between light intensity, migratory behavior of sockeye salmon *Oncorhynchus nerka* fry, and predation by cottids *Cottus* spp. We tested the hypothesis that above-natural intensities of nighttime light would increase cottid predation of sockeye salmon fry. In circular tank experiments under controlled laboratory conditions, we tested the ability of cottids to prey on sockeye salmon fry under six different light intensities using minimal water circulation to separate the effect of the migratory behavior of fry from the ability of cottids to capture them. We found that cottids preyed most effectively in complete darkness, whereas the lowest predation occurred at the brightest light intensity. We next tested the predation ability of cottids at four light intensities in a pair of artificial streams to simulate more natural conditions. In experiments without cottids, the majority of fry passed quickly through the artificial streams under complete darkness, but as light intensity was increased, fewer fry emigrated and did so at a slower rate. With cottids present and increased light intensity, even fewer fry emigrated but they did so at a faster rate than did those in the stream without cottids. We determined that cottids probably consumed about 5% of the sockeye salmon fry under complete darkness and ate about 45% of the fry at the brightest light intensity tested. In experimental field trials, the shoreline abundance of fry and predation by cottids increased as light intensities increased. Using two small lights within an 8-m shoreline section on the Cedar River, Washington, we delayed as many as 550 sockeye salmon fry and observed predation of as many as 7.6 fry/cottid. At the end of the experiment, we turned the lights off and noted that the shoreline abundance of fry declined dramatically. At two locations on the Cedar River lit by city lights, the abundance of sockeye salmon fry and predation by cottids was substantially greater than at nearby sites with low light. Also, we demonstrated at one site that reducing light intensity substantially reduced predation on sockeye salmon fry. Overall, we conclude that increased light intensity appears to slow or stop out-migration of fry, making them more vulnerable to capture by predators such as cottids.

After emerging from their redds, most sockeye salmon *Oncorhynchus nerka* fry immediately emigrate downstream at night to a lake environment, where they reside for the next year. However, during this brief (usually one or two nights) out-migration period, predation by other fishes can be an important source of mortality (Foerster 1968; Beauchamp 1995). Fry presumably reduce their vulnerability to predators by emigrating at night and selecting areas of the river channel with the fastest current velocities (McDonald 1960). The downstream migration of sockeye salmon fry is closely related to light intensity (McDonald 1960). The nightly downstream migration is initiated after the light intensity is less than 0.1 lx. Therefore, increased light intensity from artificial lighting may alter the migration patterns of sockeye salmon fry and change their vulnerability to predation.

The few studies that have examined predation

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on juvenile salmonids under different light intensities have had variable results. Ginetz and Larkin (1976) found that predation of sockeye salmon fry by rainbow trout *O. mykiss* in artificial streams increased as light intensity was increased under low light conditions (<0.1 lx); at high light intensities (0.5–3.0 lx), however, predation decreased as the light intensity was increased. Predation of chum salmon *O. keta* fry by staghorn sculpin *Leptocottus armatus* increased with increased light intensity at night but decreased with increased light intensity during the day (Mace 1983). Patten (1971) found that predation on coho salmon *O. kisutch* fry was greater on moonlit nights than on moonless nights; their results may have been biased, however, by differences in water temperature between treatments. In contrast, Petersen and Gadomski (1994) found that predation on chinook salmon *O. tshawytscha* smolts by northern pikeminnow *Ptychocheilus oregonensis* increased as light intensity decreased from 215 to 0.01 lx.

With increased urbanization and development of the Pacific Northwest, the amount of artificial lighting has increased on many streams. The effects of artificial lighting on salmonid populations is poorly understood. In Washington, the Lake Washington sockeye salmon are found within a large urban area. The major spawning tributary to Lake Washington is the Cedar River, some sections of which are exposed to artificial lighting and also present migration routes for sockeye salmon fry. In recent years, sockeye salmon production has declined in the Cedar River; increased predation on migrating sockeye salmon fry as a result of increased nighttime lighting may be one factor in the decline of the Cedar River sockeye salmon population.

The objective of this study was to determine the effect of light intensity on the migratory behavior of sockeye salmon fry and on the predation of fry by cottids *Cottus* spp. in the Cedar River.

Study Site

The Cedar River, the main tributary for the Lake Washington basin (Figure 1), is the major spawning area for sockeye salmon. The lower 35.1 km are accessible to anadromous salmonids. Landsburg Dam, a water-diversion structure, prevents fish from migrating farther upstream. The lower 3 km of the Cedar River flows through a large, heavily urbanized floodplain. This river section is within the City of Renton, Washington, and has numerous sources of artificial light from urban and residential development. Upstream of river kilometer (rkm) 3, the river valley has some residential development but artificial light is substantially less than in the Renton area. Historically, the Cedar River did not flow into Lake Washington but flowed south as part of the Duwamish River. In 1917, however, the Cedar River was diverted into Lake Washington and a ship canal was constructed to connect the lake to Puget Sound. The historical abundance of sockeye salmon in the Cedar River is poorly understood, although the current sockeye salmon population in the Cedar River appears to be derived principally from introductions between 1937 and 1945 of fry from Baker Lake, Washington (Hendry et al. 1996).

Lake Washington, a large monomictic lake with a total surface area of 9,495 ha and a mean depth of 33 m, sits within a large urban area that includes both Seattle and Renton. More than 78% of the shoreline is given over to residential land use. The lake supports a large run of sockeye salmon. Some years have seen adult returns in excess of 350,000 fish, with most of the adult fish spawning in the Cedar River.

After emerging from the gravel, sockeye salmon fry immediately migrate downstream to Lake Washington, where they reside for the next year. They migrate primarily at night but some daytime migration can occur, particularly during high-flow events with increased turbidity (Seiler and Kishimoto 1997; Hensleigh and Hendry 1998). Fry generally take one or two nights to reach the lake (Seiler and Kishimoto 1997). In the Cedar River, sockeye salmon fry are vulnerable to predation from rainbow trout (both resident and steelhead; Beauchamp 1995), cutthroat trout *O. clarki*, juvenile coho salmon, and four cottid species: coastrange sculpin *Cottus aleuticus*, prickly sculpin *C. asper*, riffle sculpin *C. gulosus*, and torrent sculpin *C. rhotheus* (Tabor et al. 1998).

Prickly sculpin is the largest cottid in Lake Washington and the Cedar River, reaching more than 225 mm total length (TL). Prickly sculpin that prey on sockeye salmon fry in the Cedar River are generally 50–150 mm TL (R. Tabor, unpublished data). Larger prickly sculpin mostly consume larger prey such as lamprey (adults and ammocoetes) *Lampetra* spp., adult longfin smelt *Spirinchus thaleichthys*, other cottids, and signal crayfish *Pacifastacus leniusculus*. Found in quiet areas of the lower 5 km of the Cedar River, prickly sculpin are also the dominant cottid in the benthic areas of Lake Washington (Eggers et al. 1978).

Torrent sculpin and riffle sculpin are widespread

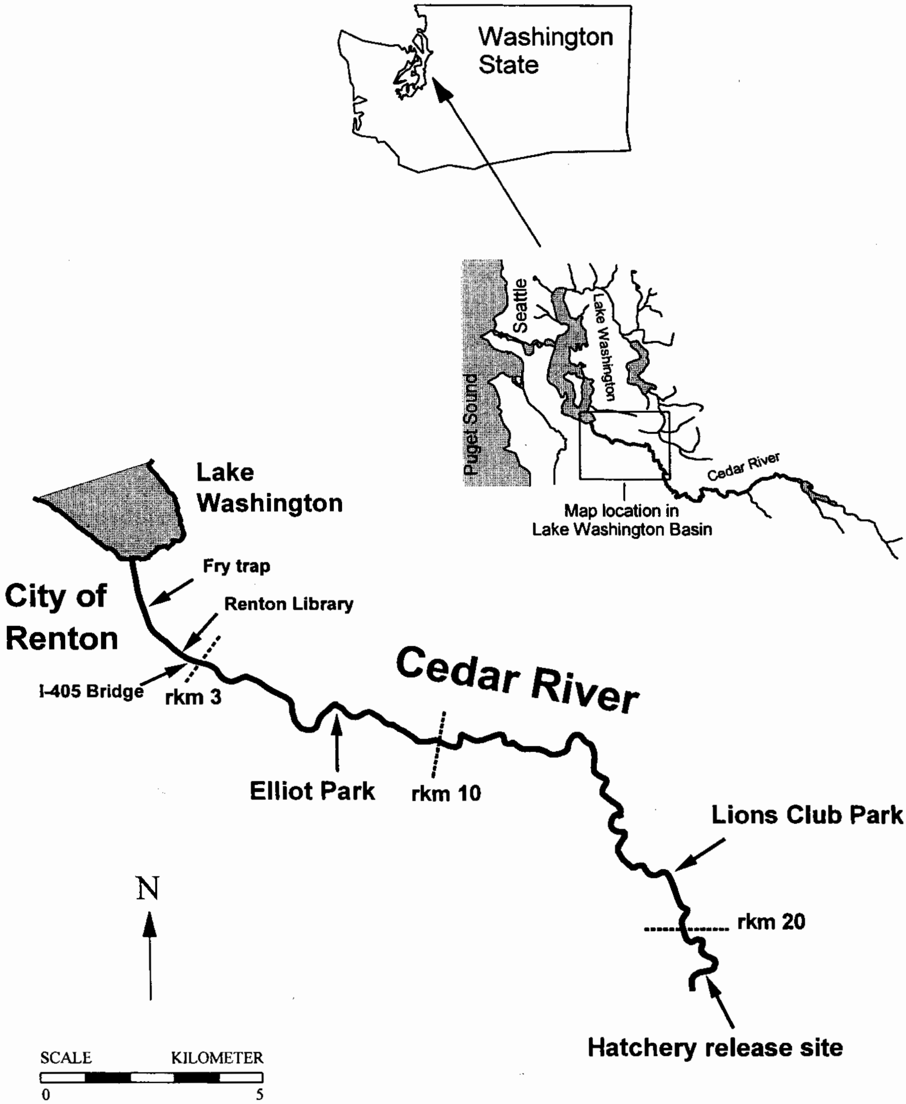

FIGURE 1.—Map of the lower Cedar River, showing the two experimental field trial sites (Lions Club Park and Elliot Park) and the two Renton city light sites (Renton Library and I-405 bridge). The locations of the release site for hatchery sockeye salmon fry and the fry enumeration trap are also shown. rkm = river kilometer.

in the Cedar River, inhabiting the lower 55 km of the river and several small tributaries. Coastrange sculpin occur primarily in the lower 21 km of the river. Torrent sculpin as large as 150 mm TL have been found in the Cedar River. Because of their high abundance and relatively high predation rates, torrent sculpin appear to be the most important cottid predator of sockeye salmon fry in the Cedar River (Tabor, unpublished data). Sizes of riffle sculpin and coastrange sculpin in the Cedar River are generally similar, both reaching approximately 120 mm TL. Riffle sculpin are typically found in low-velocity areas along the shore of the Cedar River. Coastrange sculpin are usually found in riffles; however, large individuals are often found in pools.

Methods

To determine the effect of light intensity on the migratory behavior of sockeye salmon fry and on the predation of fry by cottids, we conducted several laboratory experiments and field studies (Table 1). We also measured light intensity at sites along the Cedar River to document the amount of

TABLE 1.—List of various study components used to examine the relationship between light intensity and sockeye salmon fry migratory behavior and predation by cottids. All field studies were conducted on the Cedar River. The cottid species of the field studies are listed in order of abundance; river km is distance from the mouth of the river.

Study component	River km	Dates	Cottid species
Laboratory experiments			
Circular tank experiments		May 1997	Prickly and torrent sculpin
Artificial stream experiments		May, Jun 1997	Prickly sculpin
Field Studies			
Experimental field trials			
Lions Club Park	18.3	Mar, Apr 1999	Torrent and riffle sculpin
Elliot Park	7.4	Apr, May, Jun 1999	Torrent, coastrange, and riffle sculpin
Renton city lights			
Renton Library	2.4	Mar 1999, Feb 2001	Coastrange sculpin
I-405 bridge	2.7	Feb 1998, Feb 2001	Coastrange and torrent sculpin
Light intensity readings			
City of Renton	0.0–2.9	Mar, Oct 2000	
Non-lighted areas	0.5–13.2	Feb, Apr 2001	

artificial lighting present and to assess how much the moon and cloudy nights affect light intensity levels. We used cottids to test the effect of increased light intensity on predation of sockeye salmon fry because cottids readily adapt to laboratory conditions, are abundant, and are important predators of sockeye salmon fry in the Cedar River (Tabor et al. 1998). Prickly sculpin and torrent sculpin were used in the laboratory experiments; torrent sculpin, coastrange sculpin, and riffle sculpin were collected at the field study sites.

Laboratory Experiments

We took a dual experimental approach to determine whether cottids prey more effectively at the light intensities generated by standard artificial light sources. Because cottids and sockeye salmon fry may alter their behavior in relation to light intensity, the sensory abilities of one to detect the other may be differentially affected by light intensity. We first tested predation of cottids in the simplistic environment of circular hatchery tanks with minimal water flow, to allow us to separate the effect of the changes in fry migratory behavior that might occur under different light intensities from the ability of cottids to prey on them. To assess the effect of light intensity on sockeye salmon fry behavior, we performed a second experiment, using artificial streams under more natural conditions that allowed fry to migrate downstream. The sockeye fry released upstream in these trials could behave more naturally in this environment than in a hatchery tank in relation to the light intensities used in our treatments; that is, they could migrate quickly through the artificial stream or delay their passage by stationing in eddies or burying in the gravel substrate.

During May–June 1997, we conducted experiments at the Western Fisheries Research Center, U.S. Geological Survey, Seattle, Washington. Prickly sculpin (74–103 mm TL) and torrent sculpin (74–98 mm TL) collected from the Cedar River and Lake Washington by electrofishing were transported to the laboratory, where they were maintained in circular holding tanks in size-sorted (small: 70–79 mm TL; medium: 80–89 mm TL; and large sculpin: 90–99 mm TL) and species-specific groups. The sizes of cottids collected are representative of those that commonly consume sockeye salmon fry in the Cedar River (Tabor, unpublished data). Sockeye salmon fry were obtained periodically from the Washington Department of Fish and Wildlife fry enumeration trap located near the mouth of the Cedar River. The mean fork length (FL) of the fry was 28.4 mm (N = 90; SE, 0.18; range, 26–34 mm FL). The fry were presumably both migration- and predator-experienced. After transport to the laboratory, the fry too were held in circular holding tanks. Fry were fed commercial fry food daily throughout the experimental period. Most fry were used in experiments within 5 d after they were collected; however, some fry used in the last experiments were held as long as 14 d. Sculpin were fed available salmonid fry before the experiment.

The light intensities used in the experiments represent the range of values observed during field measurements in the lower Cedar River. All light intensity measurements were made with an International Light, Inc., model IL1400A radiometer/

photometer. The light source consisted of one or two strings of small ornamental lights (small, clear, holiday tree lights) taped to the underside of the lids of the tanks and the artificial streams and suspended directly above the water. Each light string was connected to an outlet box and a dimmer switch. Predation trials in both experiments were run during daylight hours. Testing environments were covered with layers of black sheeting to exclude all light except that produced by our artificial light source.

Circular tank experiments.—The tank experiments were conducted in three 1.2-m-diameter circular tanks. Water depth was maintained at 30 cm and water temperature was approximately 12°C. We tested six light intensities (0.00, 0.03, 0.06, 0.11. 1.08, and 10.8 lx) during the predation experiments. For each trial, we randomly selected one of these treatment light intensities. We carefully adjusted the lights to maintain that intensity in each of the three replicate test tanks before each experimental trial. In each trial we used single-species groups of 20 sculpin (three large, nine medium, and eight small fish randomly sampled from the size-sorted holding tanks) and 100 fry. We performed six replicate trials for each light intensity with both prickly sculpin and torrent sculpin. The fry were given 15 min to adjust to the experimental setup before the sculpin were added. Two black Plexiglas shelves within each tank served as a refuge/hiding place for the sculpin during the experiments. After addition of the sculpin, each trial lasted 40 min. Trial starting times were staggered for the three test tanks to allow sufficient time for recovery of all fish with a small aquarium net and flashlight. Predation was determined as the number of sockeye salmon fry lost during a trial. Results of the light intensity experiment were analyzed with one-way analysis of variance (ANOVA) tests and post hoc Tukey's Honestly Significant Difference (HSD) tests.

Prickly and torrent sculpin were used on alternate days to allow adequate digestion time between trials. The stomach contents of three replicate groups of cottids from both the 0.00 and 10.8 lx light intensities (N = 60 for each light treatment and cottid species combination) were removed by gastric lavage to confirm consumption of fry, determine the percent of sculpin that consumed fry, and confirm the absence of previously consumed fry. Light et al. (1983) found gastric lavage was 100% effective for removing stomach contents of slimy sculpin *C. cognatus*.

Artificial stream experiments.—Sockeye salmon fry migration/behavior experiments were done in two identical artificial streams containing natural river gravel substrate. Each stream was 9 m long by 1.5 m wide and was contained within a fiberglass trough. We used only a 3-m section of each stream to allow enough space downstream to set up a fish trap for collecting the fry. Each experimental section consisted of a 2.5-m-long pool and a short riffle section. The riffles had a 2% gradient and a water depth of 18 cm. The maximum depth of each pool was approximately 75 cm. Surface velocities ranged from 0.37 m/s near the inflow to 0.12 m/s at the outflow. Near the bottom of each pool the water velocity was negligible. The light intensity was measured approximately 10 cm below the surface of the water in both streams. For the predator trials, 20 prickly sculpin (mean, 86.5 mm TL; range, 75–99 mm TL) were placed in each artificial stream, where they remained throughout the duration of the experiment. We performed trials once every 2–3 d to allow the sculpin enough time to digest fry from the previous trial.

At the start of each trial, 125 fry were transferred from the laboratory, where they had been held in low light intensity, and were released at the upstream end of each experimental section. Trials started immediately with the addition of fry, and the fry traps were checked with a flashlight at 20 min and after 2, 4, and 6 h. Any fry caught in the fry trap were removed with a small aquarium net and counted. After 6 h, all lights were turned off and the fry were given 12–16 h (overnight) to migrate through the streams to the trap. Again, any fry in the trap were removed and a final count was made. We did not try to collect any fry possibly remaining in the artificial streams because preliminary work had indicated the fry were extremely difficult to locate and capture. In nonpredator trials, the number of fry not accounted for by the beginning of the next trial was added to the number of fry released (125) at the start of that next trial. Consequently, the results are presented as a cumulative percentage of the total fry in each stream that migrated downstream to the fry trap within the trial periods. In the predator trials, we assumed that the fry not accounted for were all consumed by sculpin. Because few fry migrated overnight in the predator trials when the streams were darkened, this appears to be a valid assumption.

The artificial stream trials were conducted in two parts. No predators were used in the first part, in which two replicates of each of three light intensities (0.00, 1.08, and 5.40 lx) were tested. In the second part, predators were present in one stream and absent in the other, and four light intensities were tested (0.00, 0.22, 1.08, and 5.4 lx). Two replicates of each level were tested except that time constraints allowed only one trial at 0.22 lx. On each trial date, the same randomly selected light intensity treatment was used in both the predator and nonpredator artificial stream.

Field Studies

Experimental field trials.—We performed experimental field trials at two sites on the Cedar River, the Lions Club Park at rkm 18.3 and the Elliot Park at rkm 7.4 (Figure 1). The Lions Park site, with a 112-m shoreline section, had two distinct habitat types: The upper 56 m had a riprap shoreline (steep sloping banks), whereas the lower 56 m had a gravel shoreline with gradually sloping banks. The Lions Club Park was the site of two experimental trials, both conducted on nights when hatchery sockeye salmon fry had been released upstream at rkm 21.7. On March 31, 1999, 135,000 fry were released at approximately 2015 hours and on April 5, 1999, 57,000 fry were released at approximately 2115 hours. Most of the fry appeared to reach the fry trap at rkm 1.2 between 2300 and 0000 hours on March 31 and between 0000 and 0100 hours on April 6 (D. Seiler, Washington Department of Fish and Wildlife, unpublished data).

The other site, at Elliot Park, consisted of a side channel immediately downstream from the outlet of a spawning channel. We sampled the side channel five times from April 7 to June 14, 1999, during the fry out-migration period. Fry observed at this site most likely originated from the spawning channel, because no hatchery fry were released during these dates. The Elliott Park site consisted of one 40-m-long sand/gravel shoreline section.

Shoreline sections at both sites were divided into 8-m-long units. Lights were added only to every other unit to ensure that light from one experimental unit did not affect the adjacent units. Treatments were randomly assigned within the alternate shoreline sections. Two lights were used for each experimental unit, each mounted at the top of 2-m-tall poles that were placed at the far ends of each unit; there, the lights were directed toward the middle of the unit. Each light was set up as an individual light system consisting of a 60-W light bulb, a deflector to focus the light, and a dimmer switch to control the light intensity. We used different combinations of five light intensities: (1) control (no lights), 0.01–0.11 lx; (2) dim, 0.16–0.27 lx; (3) low, 0.48–0.59 lx; (4) medium, 1.08–1.51 lx; and (5) bright, 10.80–15.10 lx. Light intensity was measured at the surface of the water, 2 m from shore. Generally, we took three measurements, one in the middle and one each from just inside the upstream and downstream edges. The middle of each experimental unit was the brightest, and the upstream and downstream edges were the dimmest; moreover, light intensity attenuated across the river channel. We turned on the lights shortly after dusk and adjusted their settings to get the appropriate light intensity.

Experiments lasted 2–3 h. At both sites, sockeye salmon fry abundance was estimated by counting fry along the shoreline. Fry were counted by an observer using a flashlight, who slowly walked along the shoreline in a systematic pattern to ensure that the area out to 2 m from shore was completely covered. To be consistent between treatments, we counted only fry within the beam of the flashlight. Preliminary observations indicated that fry were in shallow water and close to the surface of the water, tended to hold their position facing into the current, and did not move appreciably. Thus, fry could be easily counted and fish counts between different shoreline types (gravel shore and rip-rap) could be compared. In subsequent electrofishing after the experimental trials, we found no evidence that sockeye salmon fry were hidden within the riprap. We assumed that the counting had a minimal effect on fry abundance because it took only a short time, approximately 1 min per shoreline section. Fry were counted every 15 min at the Lions Club Park. At Elliot Park, we only did two counts, one shortly after the experiment was started and another at the end of the experiment. For some experimental trials, we recounted the number of fry present 20 min after the lights had been turned off.

After the lights had been turned off, we used backpack electrofishing equipment to collect cottids along the shoreline to determine the level of predation. We assumed there was little movement of sculpin between sections because of the relatively short duration of each experiment (approximately 2 h) and the 8-m gap between sections. We also considered it unlikely that a sculpin from one section could flee into another section because there was a gap between sections and because we sampled in an upstream direction, from the downstream end to the upstream end. Stunned fish were collected with the aid of dip nets and a spot light. After capture, cottids were identified as to species and measured for total length. Cottids of 50 mm TL or larger were anesthetized and their stomach contents were removed by gastric lavage. Because smaller cottids rarely consume sockeye salmon fry (Tabor, unpublished data), we did not check the contents of their stomachs. Ingested fry were counted and categorized as freshly ingested or well digested. Only counts of freshly ingested fry were used in the analyses. We assumed that freshly ingested fry were consumed during the experiment, whereas well-digested fry had been consumed the previous night or sometime before the experiment. Because we started the experiments shortly after sunset and because cottids are primarily nocturnal and sockeye salmon fry migrate primarily at night, we deem this a valid assumption.

We tested differences in fry abundance with a two-way ANOVA without replication. Data were log-transformed because the data were multiplicative rather than additive (Zar 1984). The two factors paired for testing were light intensity and habitat type for the Lions Club Park data and light intensity and date for the Elliot Park data. Several cottids did not consume any fry, meaning that the predation data were not normally distributed; therefore, we used nonparametric procedures to compare predation, a Mann–Whitney U-test (two samples) or a Kruskal–Wallis test (more than two samples).

Renton city lights.—Two sites were selected in Renton, the Renton Library and the I-405 bridge (Figure 1), as having an area of high light intensity and a nearby area with similar habitat and substantially lower light intensity. Abundance of sockeye salmon fry and predation of fry by cottids were monitored on nights when hatchery sockeye salmon fry were released so we could ensure that a large number of fry were available. The Renton Library sits 5 m above the Cedar River, spanning the entire width of the river and covering a 28-m-long section of the river. We compared the findings for a 22-m-long river section under the library, where no artificial lights were present, with those for a 22-m-long river section 3 m downstream of the library and characterized by several artificial lights spanning the width of the river. The library site was sampled once in 1999 and once in 2001. The I-405 bridge had several lights under the bridge to illuminate a walkway that spans the river. The control site for this location was 180 m upstream from the bridge, where no direct lighting was present. Both sites were 20 m long. Sampling was conducted once in 1998 and again in 2001. Sampling in 2001 was conducted after artificial lights had been shielded and light intensities along the river had been substantially reduced from 9.7–21.5 lx in 1998 to 0.14–0.32 lx in 2001. In the 2001 sampling, streamflow was lower, water temperature was slightly higher, and fry abundance was greater than during the 1998 sample (Table 2). Therefore, predation in 2001 was expected to be as high or higher than during sample dates in 1998. Sockeye salmon fry abundance at all sites was estimated by counting fry along the shoreline, similar to the experimental field trials. Light intensity was measured at the surface of the water in the middle of the area sampled.

TABLE 2.—River conditions and the number of emigrating sockeye salmon fry on three dates used to examine the difference in predation of sockeye salmon fry by cottids before and after lights at the I-405 bridge were shielded. Streamflow and water temperature data were taken by U.S. Geological Survey at rkm 2.2. Fry abundance estimates were obtained from fry trap data (D. Seiler, Washington Department of Fish and Wildlife, unpublished data). The fry trap was located at rkm 1.6 (from the mouth of the river). Catch efficiency of the fry trap on the dates listed ranged from 9.6% to 10.2%.

Date	Fry abundance		Streamflow (m^3/s)	Temperature (°C)
	Sample night	Prior night		
Feb 23, 1998	296,800	318,000	16.7	7.3
Feb 25, 1998	537,900	434,000	18.6	7.2
Feb 21, 2001	684,000	557,000	10.0	7.7

At both sites, cottids were collected with backpack electrofishing equipment and analyzed for stomach content to compare the extents of predation of fry. At Renton Library, cottids were sampled along the shoreline and were collected visually with the aid of dip nets and a spot light. At the I-405 bridge site, cottids were collected in the mid-channel area because few cottids were present along the shore of the control site. Stunned cottids in the mid-channel area were collected passively with the aid of block nets. After capture, cottids were identified to species and TL was measured. Afterwards, their stomach contents were removed by gastric lavage and consumed sockeye salmon fry were counted. We assumed that cottids had consumed fry in the same general area where we captured them. We included counts of all sockeye salmon fry ingested because the artificial lighting was consistent from night to night. A Mann–Whitney U-test was used to compare differences in predation between the lighted site and the control site.

Light intensity readings.—In 2000 we assessed the artificial lighting along the lower 3 km of the Cedar River, taking light readings every 50 m over rkm 0.9–2.9. Below rkm 0.9, access to the river was limited in many areas, so additional readings were only made at rkm 0.0, 0.2, 0.3, and 0.7. All

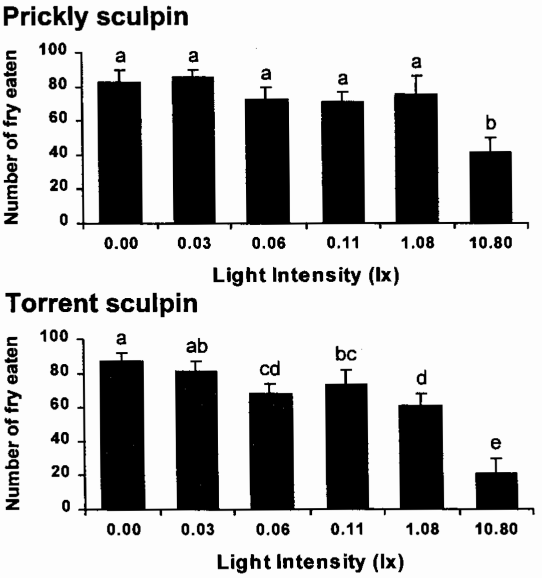

FIGURE 2.—Number of sockeye salmon fry eaten (±SD) by prickly sculpin and torrent sculpin in 40-min trials in circular tanks at different light intensities. Each bar is the mean of six trials. Groups of bars with different letters are significantly different (ANOVA and Tukey's HSD; $P < 0.05$).

readings were taken close to the riverbank, approximately 1–5 m from shore, and at the surface of the water. At major light sources, we took an additional reading to determine the maximum light intensity. Besides identifying sources of direct lighting, we also measured light intensity in other natural lighting conditions—(1) overcast skies; (2) clear skies, no moon; and (3) clear skies, full moon—at five locations without artificial lighting: rkm 0.5, 3.1, 6.9, 9.8, and 13.2.

Results

Laboratory Experiments

Prickly sculpin and torrent sculpin displayed similar amounts of predation with respect to increasing light intensity in tank experiments. Both species captured more fry under low light conditions than under the highest light intensity (Figure 2). Prickly sculpin captured a mean of 82.3 fry (SD = 7.4) at 0.00 lx compared with a mean of 41.5 fry (SD = 8.7) at 10.80 lx. Torrent sculpin captured a mean of 86.8 fry (SD = 5.3) at 0.00 lx and a mean of 21.3 fry (SD = 8.3) at 10.80 lx. A separate one-way ANOVA was performed on untransformed data of number of fry eaten for the two sculpin species. The ANOVA tests indicated significant differences among the six light intensities tested for both prickly sculpin ($P < 0.001$) and torrent sculpin ($P < 0.001$). Results from a post hoc Tukey's HSD test for prickly sculpin showed significantly less fry consumption at the highest light intensity but no difference among the other five light levels (Figure 2). Torrent sculpin indicated more differences among the six light intensities although, as with prickly sculpin, predation at the highest light intensity differed from that at the other five. The other five levels showed significant differences between treatments ($P < 0.05$), but there was no consistent trend from the lowest intensity to the highest one. In general, however, the number of fry eaten by torrent sculpin decreased as the light intensity increased.

Gastric lavage of three replicate trials of 20 sculpins each (total, 60 sculpin per species) from the trials at 0.00 and 10.80 lx verified that both prickly sculpin and torrent sculpin consumed more sockeye salmon fry at the lowest light intensity than at the highest light intensity. Ninety-five percent of the prickly sculpin had consumed at least one fry at 0.00 lx, whereas only 87% consumed fry at 10.80 lx. Thirty-eight percent of the prickly sculpin had consumed more than four fry at 0.00 lx, but only 5% had consumed more than four fry at 10.80 lx. The maximum number consumed by a prickly sculpin was nine fry (0.00 lx). Ninety-two percent of the torrent sculpin had consumed at least one fry at 0.00 lx, but only 68% had consumed fry at 10.80 lx. Fifty-two percent of the torrent sculpin had consumed more than four fry at 0.00 lx, whereas only 7% had consumed more than four fry at 10.80 lx. The maximum number of fry consumed by a torrent sculpin was 12 fry (0.00 lx).

We also verified that 2 d was sufficient time for digestion of previously consumed fry (and therefore, resumption of predatory motivation) in these experiments because only freshly consumed fry were recovered in the gastric lavage contents.

Artificial Stream Experiments

The first set of experimental trials, conducted with no predators present, indicated that sockeye salmon fry migrated through the stream at a faster rate under complete darkness (0.00 lx) than in the other two light intensities (1.08 and 5.4 lx). Under complete darkness, 74% (SD = 4.5%) of the fry migrated downstream within the first 20 min of the trials, and an additional 25% migrated downstream over the course of the next 24 h. Results were similar for the two treatments with light present but differed from those with light absent. In the 1.08 and 5.40 lx trials, 32% (SD = 8.6%) and 34%

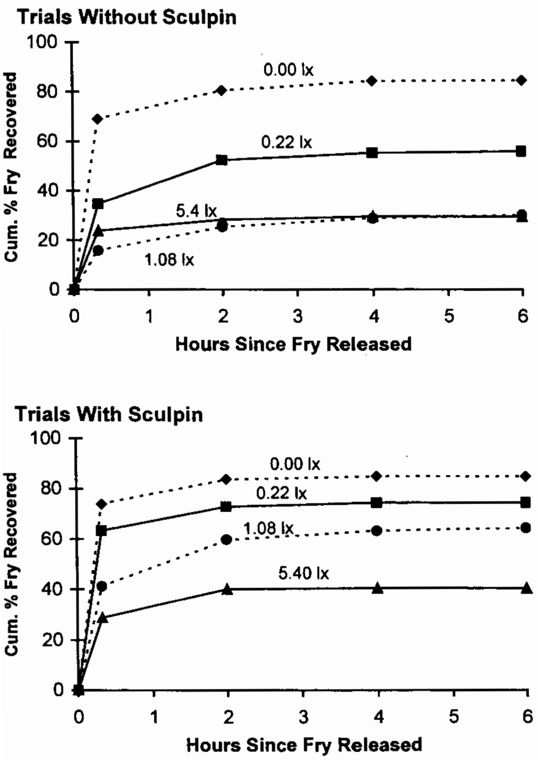

FIGURE 3.—Cumulative percent of total sockeye salmon fry recovered after release in artificial streams under four different light intensities. Each line is the mean of two trials, except that only one trial was conducted for the 0.22-lx experiment. The top and bottom panels show the results for trials when fry emigrated in the absence or in the presence of prickly sculpin, respectively.

(SD = 7.8%), respectively, of the fry migrated downstream within the first 20 min, and an additional 52% and 56%, respectively, migrated downstream within the next 24 h.

The second set of experimental trials was conducted with sculpin present in one stream and not in the other. These predation plus out-migration trials showed several strong patterns, even with only two trials completed at each of four light levels (Figure 3). First, as in the earlier trials, fry readily emigrated through the artificial streams under complete darkness but increasingly delayed passage as the light increased. Second, fry emigrated faster in all nondark trials when sculpin were present. Third, and most crucial, a greater proportion of fry were never recovered in the stream trials with sculpin present and the proportion missing was related directly to the light intensity (Table 3). Even though fry migrated more quickly with sculpin present than when the predators were absent, the fry were apparently more vulnerable to predation with increasing light intensity. At the most intense light tested (5.4 lx), subtracting the average number of fry unaccounted for in all trials with no sculpin present (10%) indicates that about 45% of the fry in the trial were probably consumed by sculpin. At 0.22 lx, about 28% of the fry became prey, and only about 5% were likely prey to the sculpin in the dark trials. Finally, our results consistently showed that fry not recovered in the first 2 h of a trial including sculpin were never recovered.

TABLE 3.—Percentage of sockeye salmon fry not recovered from outmigration trials in the artificial streams in the presence or absence of prickly sculpin under different light intensities. Estimates of the percent eaten were derived by subtracting the mean percent fry not recovered from the trials with no sculpin (mean = 10.0%) from each mean of percent fry not recovered with sculpin present.

	Percent fry not recovered (SD)			
Light level (lx)	Sculpin absent	Sculpin present	Estimated percent eaten	Number of trials
0.00	8.1 (2.2)	15.2 (2.3)	5.2	2
0.22	13.4	38.4	28.4	1
1.08	10.0 (1.7)	34.0 (6.2)	24.0	2
5.40	8.5 (1.5)	55.2 (13.6)	45.2	2

Field Studies

Experimental field trials.—At Lions Club Park on March 31 and April 5, 1999, few sockeye salmon fry were observed in all units for the first 45 min to 1 h. Within the next 20 min, however, the number of fry increased dramatically. For example, in the brightest light experimental unit, the number of fry changed from 27 at 2025 hours to 577 at 2045 hours. This increase in the number of fry most probably resulted from the large number of hatchery fish released earlier that evening. Experimental units with greater light intensities had significantly more fry in both experimental trials (ANOVA; March 31, $P = 0.02$; April 5, $P = 0.005$; Figure 4). Moreover, within each light intensity trial, more fry were found in the gravel shore than on the riprap shore (ANOVA; March 31, $P = 0.04$; April 5, $P = 0.03$; Figure 4). On average, gravel shores had 5 times as many fry as riprap shores for a given light intensity.

Overall, fry abundance results at the Elliot Park side channel followed patterns similar to those at Lions Club Park. Fry counts were conducted on five dates; on May 3, 1999, however, the light system for the medium-light experimental unit

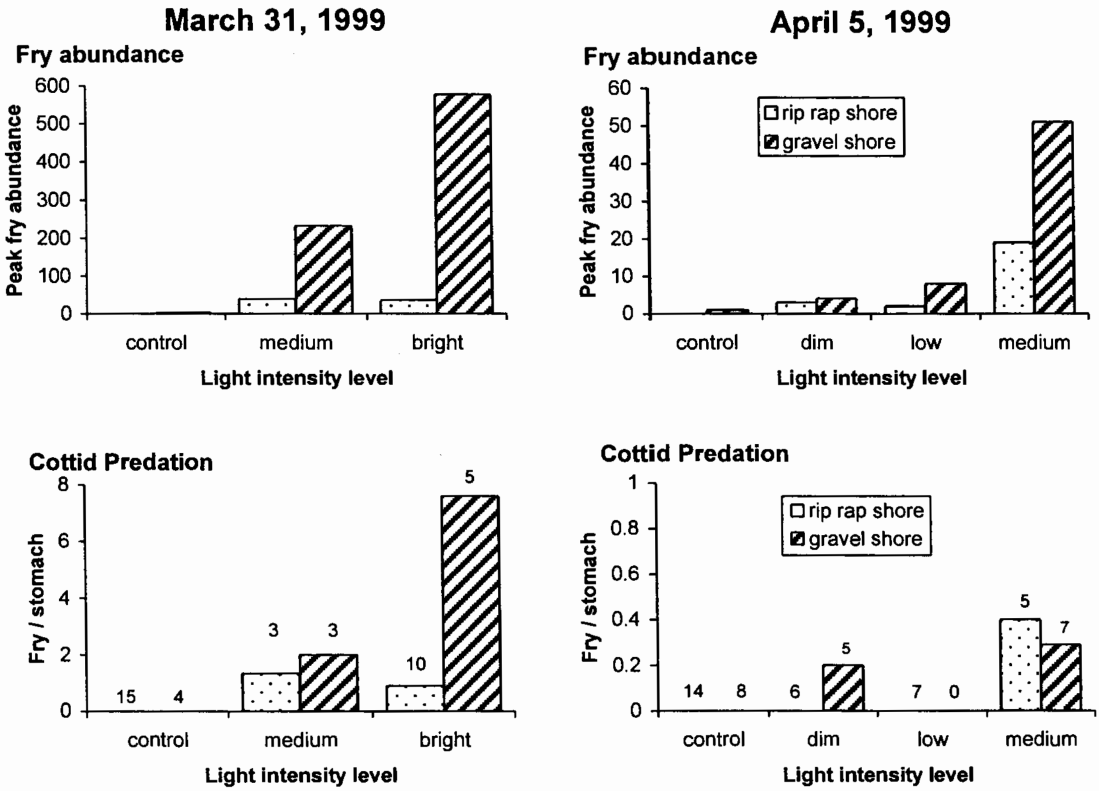

FIGURE 4.—Sockeye salmon fry abundance and cottid predation of fry at various light intensities and two habitat types from two experimental trials at Lions Club Park (rkm 18.3) on the Cedar River in 1999. Numbers above the bars indicate the number of cottid stomachs examined. Only freshly ingested sockeye salmon fry were counted as indicators of recent ingestion.

malfunctioned, and we were unable to get a fry count for that part of the experiment (Figure 5). The abundance of fry in the side channel varied greatly on the five dates sampled and most probably consisted of migrants from the spawning channel. Peak out-migration appeared to occur around May 3. An ANOVA revealed a significant difference ($P < 0.001$) in fry abundance between light intensity values and between sampling dates ($P < 0.001$). The most fry were always in the medium-light unit, the dim-light unit always had the second most numerous fry, and the control unit always had the least (Figure 5).

In two experimental trials, we also examined the abundance of fry shortly after the lights were turned off. In all the lighted experimental units, the number of fry decreased dramatically after the lights were turned off (Figure 6). In control units (no light added), the number of fry decreased slightly or actually increased. The lighted shoreline sections averaged a 93% reduction in fry abundance at Lions Club Park and a 88% reduction at Elliot Park.

In general, predation of fry by cottids showed the same trend as fry abundance. The most predation took place in experimental units with increased light. This trend was particularly noticeable during the March 31, 1999, trial at the Lions Club Park. Whereas no predation was detected in the control units, large numbers of fry were found in the stomach samples of cottids collected from the bright-light experimental unit (Figure 4). Three torrent sculpin collected from this unit had 10 or more fry in their stomachs. The maximum number of sockeye salmon fry consumed by an individual fish was 13 (92 mm TL, torrent sculpin). Differences in predation were marginally significant (Kruskal–Wallis test = 5.7, $P = 0.058$) between experimental units but were not significant between medium and bright experimental units (Mann–Whitney U-test = 3.5, $P = 0.23$). Predation in both of the lighted riprap experimental units

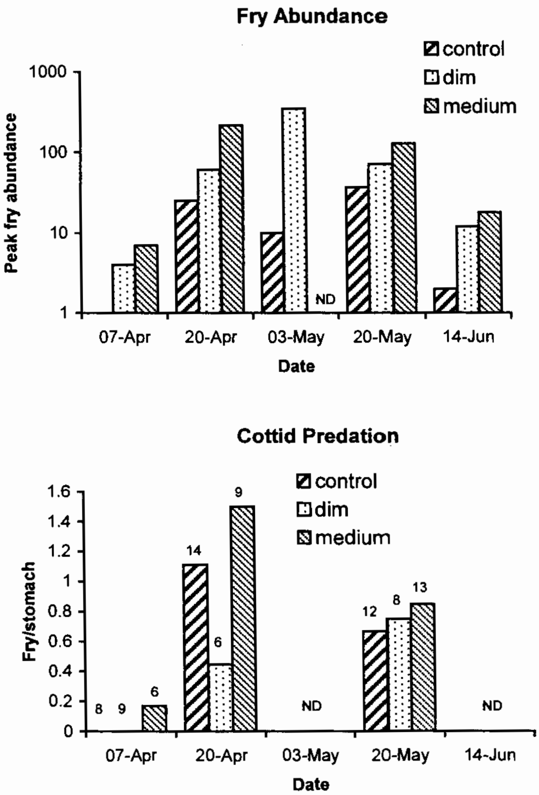

FIGURE 5.—Abundance of sockeye salmon fry (log scale) and extent of cottid predation of fry at three light intensity values on five nights in 1999 at the Elliot Park side channel (just below a spawning channel). Numbers above the bars indicate the number of cottid stomachs examined. Only freshly ingested sockeye salmon fry were counted as indicators of recent ingestion. ND = no data.

was less than in units with gravel shores; these differences were significant between the two bright experimental units (Mann–Whitney U-test = 8.0, P = 0.03) but not in the medium-light experimental unit (Mann–Whitney U-test = 3.5, P = 0.66).

Predation of fry on April 5, 1999, was low for all experimental units. Only 3 of the 42 cottids analyzed had consumed sockeye salmon fry. Although we detected no differences between treatments, four of the five fry consumed were from the medium-light experimental units and no predation was observed in the control units (Figure 4).

Cottids were collected on three occasions at the Elliot Park side channel. In each trial, the most predation was observed in the medium-light unit (Figure 5); however, no significant differences between the light intensity units were detected.

At Lions Club Park, torrent sculpin made up 92% of the cottids captured, riffle sculpin 8%. At the Elliot Park side channel, 50% of the cottids were torrent sculpin, 26% were coastrange sculpin, and 24% were riffle sculpin. Predation was observed in all cottid species present at both sites.

Renton city lights.—At both locations examined, the abundance of sockeye salmon fry along the shoreline was substantially greater at sites with high light intensity than at a nearby site with low light (Figures 7 and 8). Additionally, little predation was observed in control areas with low light intensity, whereas relatively high predation was observed in lighted areas. At the Renton Library, predation on both sample dates was significantly higher in the lighted area than in the control area (Mann–Whitney U-tests: March 18, 1999, U = 63, P = 0.03; February 21, 2001, U = 247, P = 0.002). Combined, 53% of the cottids in the lighted area had consumed sockeye salmon fry, whereas only 3% had in the control site. All of the cottids collected at the library location were coastrange sculpin.

At the lighted I-405 site on February 25, 1998, 53% of the cottids had consumed fry (0.9 fry/stomach), but no predation had occurred at the control site. Predation was significantly greater in the lighted area (Mann–Whitney U-test = 58.5; P = 0.002) than in the control area. Preliminary sampling was also done at the I-405 bridge on February 23, 1998 (the control site was not sampled). From 15 cottids collected, a total of 18 sockeye salmon fry was found in the stomach samples (1.2 fry/stomach). Shielding lights under the I-405 bridge greatly reduced light intensities in the river, consequently greatly decreasing the shoreline abundance of fry and the predation of fry. In 2001, in contrast to the sampling in 1998, the number of fry at the bridge was similar to the number at the control site (Figure 8). We sampled 22 cottids from the I-405 bridge site and 14 cottids from the control site and observed no predation at either site. Predation of fry was significantly less at the I-405 bridge site when the lights shielded than on two dates in 1998 when the lights were shining directly on the river (Mann–Whitney U-test = 319; P < 0.001). Of all the cottids collected at the bridge and control site, 96% were coastrange sculpin and 4% were torrent sculpin; both species were observed to have ingested sockeye salmon fry.

Light intensity readings.—Surveys of the lower 3 km of the Cedar River indicated that most of

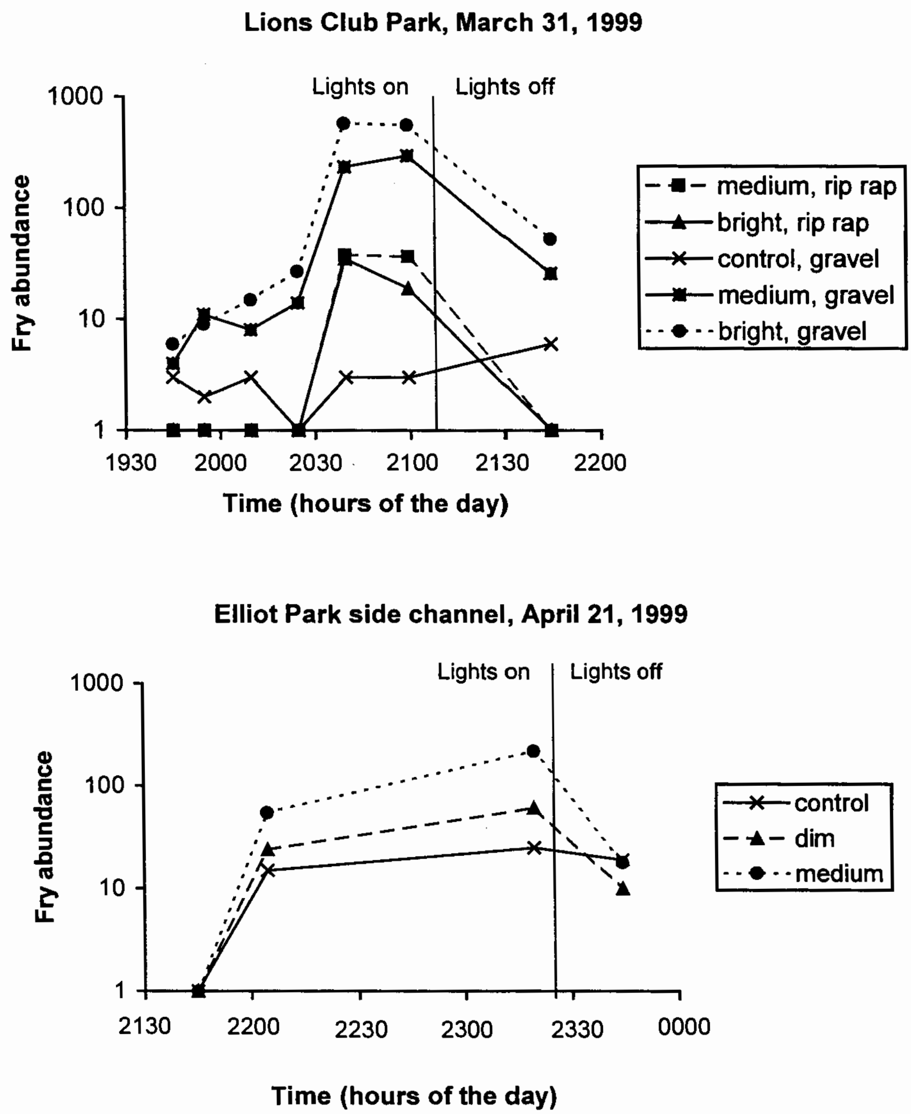

FIGURE 6.—Abundance of sockeye salmon fry (log scale) at three light intensity values in two experimental trials in the Cedar River, 1999, in which artificial lights that were on at dusk were later turned off. Vertical lines indicate when the lights were turned off. The March 31 trial was done at two habitat types, riprap and gravel shore. No fry were seen in the control riprap unit, so that site is not plotted on the graph.

this area has light intensity values (>0.2 lx) exceeding natural amounts (0.0 lx). Within the lower Cedar River, nine locations had light intensity greater than 1.1 lx. At six of these sites, the light was from street lights at bridges; at the other three, the light was associated with a building adjacent to the river. The highest light readings recorded were at the I-405 bridge (21.5 lx) and the Renton Library site (20.4 lx). Between rkm 0.9 and 2.9, the median light intensity level was 0.37 lx on a clear, moonless night but 0.94 lx on a cloudy night.

Light readings of areas with no direct lighting in the lower 13 km of the Cedar River indicated that light reflected off clouds was greatest near the mouth of the river and gradually decreased at upstream locations (Figure 9). Light intensities on cloudy nights in the lower 9 km of the river exceeded those on a clear night with a full moon. As expected, light intensity readings during clear skies were similar between locations. Observations from a plane at night suggest that most of the reflected light comes from the City of Renton

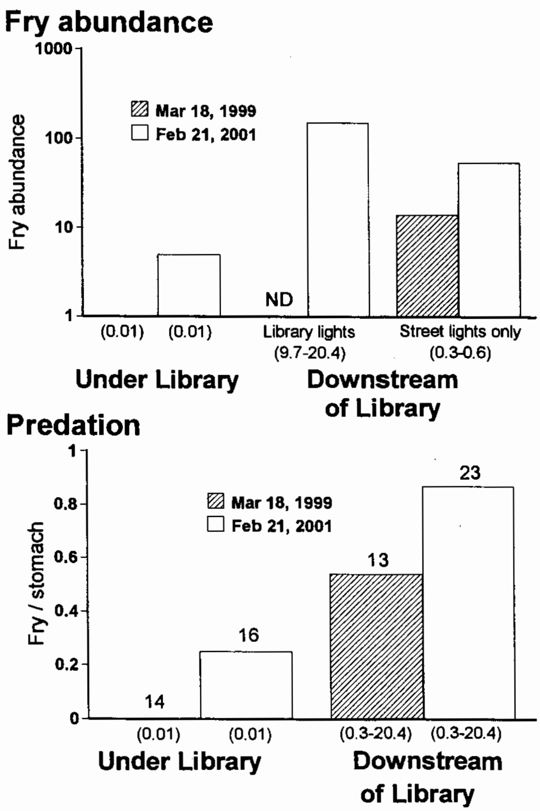

FIGURE 7.—Abundance of sockeye salmon fry (log scale) and extent of predation of fry by cottids at the Renton Library, City of Renton, Washington. The library lights were on for approximately 3 h after sunset and then turned off, whereas the street lights remained on all night. The abundance of fry was the number along a 22-m shoreline section at each site. Light intensities (in lux) are indicated in parentheses. The number of cottids examined for fry consumption is given above each bar. ND = no data.

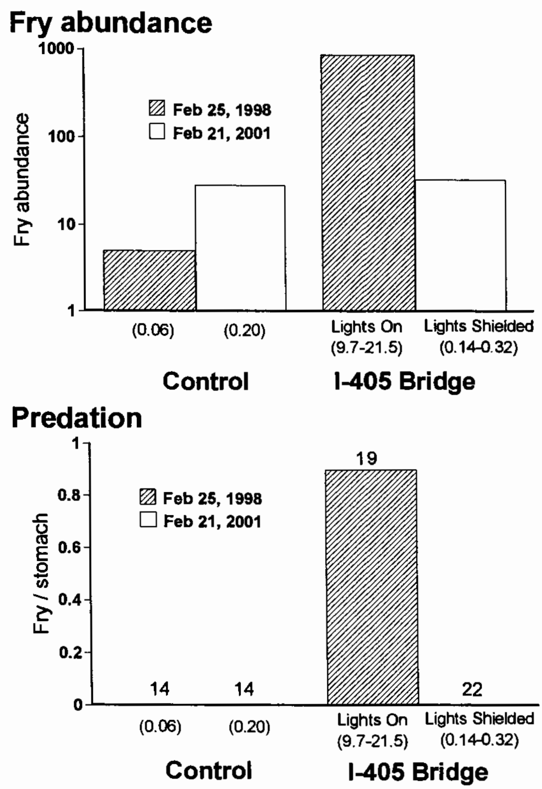

FIGURE 8.—Abundance of sockeye salmon fry (log scale) and predation of fry by cottids at two Cedar River sites with various light intensity values near the I-405 bridge, City of Renton, Washington. The abundance of fry was the number counted along a 20-m shoreline section at each site. Light intensities (in lux) are indicated in parentheses. In 1998, the lights under the I-405 bridge shone directly on the river; in 2001, the lights were shielded so that they shone primarily on a walkway and not on the river. The control site was located 180 m upstream of the bridge. The number of cottids examined for fry consumption is given above each bar.

and from a large industrial area just south of Renton. Upstream of the City of Renton, no significant lighting sources were apparent that would increase the amount of reflected light along the river during cloudy nights.

Discussion

Fry Behavior

Increasing light intensity appeared to affect greatly the behavior of sockeye salmon fry. Sockeye salmon fry usually emigrate at night, when light levels are less than 0.1 lx, and select areas of the river channel that have the fastest current velocities (McDonald 1960). Our experimental field trials demonstrated that if fry encounter lighted areas, many will hold their position in low-velocity water and delay their migration. McDonald (1960) also observed that sockeye salmon fry stopped swimming downstream when they encountered a light. Shoreline observations in the Cedar River indicated that fry were in shallow water close to the surface of the water and tended to hold their position facing into the current without moving appreciably. Our behavioral observations at lighted areas were similar to daytime observations of Hartman et al. (1962), who found that sockeye salmon fry accumulate and hold along the stream edges and invariably remain in the top 0.15 m of the water. Hensleigh and Hendry (1998) experimentally found that most fry moved down-

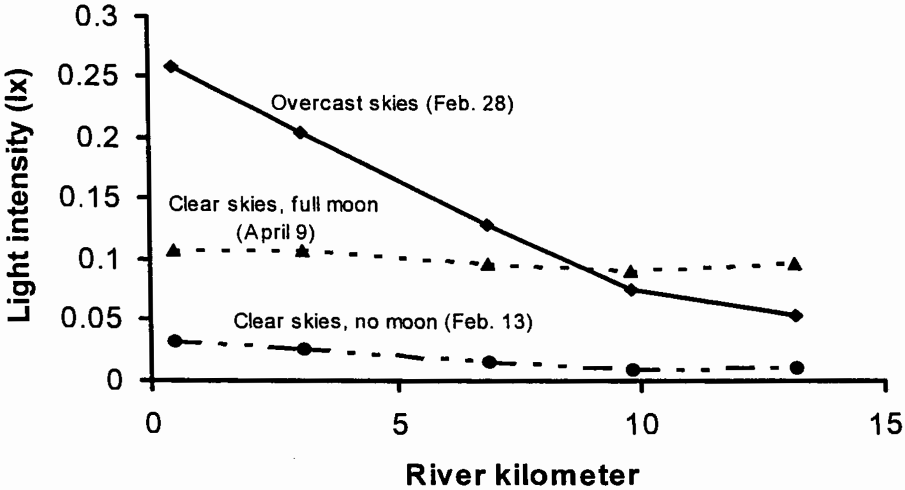

FIGURE 9.—Nighttime light intensities at five locations on the lower Cedar River as determined in 2001 under three different scenarios. Light readings were taken close to the surface of the water at locations with no direct lighting. The dates on which the light readings were taken are indicated in parentheses.

stream in the dark but tended to hold their positions or move slightly upstream in the light.

As shown by counts of fry along the shoreline of the Cedar River, the abundance of sockeye salmon fry that were delayed appeared to be positively related to the light intensity. Even small increases in light intensity seemed to affect fry behavior. At Elliot Park, for example, we consistently observed differences in fry abundance between the control (0.11 lx) and the dim-light experimental unit (0.22 lx). In the Cedar River, other variables such as total number of nightly migrants, water velocities, shoreline type, substrate type, streamflow, and turbidity will probably also influence the number of fry delayed. If these other variables could be held constant the number of fry delayed will probably be closely related to light intensity values.

We were surprised by the large number (>550 fry) of sockeye salmon fry present within the bright-light experimental unit (sand and gravel shoreline) during the March 31, 1999, experiment. Approximately 120,000 fry had been released on that date. Assuming a similar per kilometer survival rate as those in hatchery releases from Landsburg Dam (Seiler and Kishimoto 1997) and if the number of wild fry was minimal, we estimate that 110,000 hatchery fry moved past our experimental site. Therefore, we were able to delay 0.5% of the release group within an 8-m-long shoreline section with two small lights. Near the shoreline, the light intensity level was 11–15 lx, but in the middle of the channel, where most fry would be, we would expect the light intensity to be only 0.1 lx. This suggests that several large lights spread out over a long section of shoreline and across the river channel could strongly affect the behavior of outmigrating fry.

The duration of delay for an individual sockeye salmon fry is unclear. We assumed that once a fry is delayed in a lighted area, it may be delayed for a considerable period of time. At the I-405 bridge site (before the lights were shielded), we routinely observed large numbers of fry at different hours of the night, from shortly after dusk to shortly before dawn. Although there may have been some level of turnover of individuals, we think it reasonable that many were delayed for several hours. Because fry only take one or two nights to reach Lake Washington, a delay of a few hours may markedly increase their risk to predation. McDonald (1960) was able to completely stop the nightly movement of sockeye salmon fry with artificial lighting (30 lx) that was kept on all night. In other experimental trails, McDonald (1960) turned the lights off at different times of the night and observed that immediately afterwards the migration of fry commenced. In our experimental field trials, the fry appeared to resume their migration shortly after the lights were turned off. Further experiments are needed to determine how long fry are delayed.

In addition to increased shoreline abundance of sockeye salmon fry, increased light intensity may also cause fry to move into low-velocity areas along the bottom of the river channel. Once fry encounter artificial lighting, they reverse their direction and face upstream into the current (McDonald 1960); they will either stay in fixed position above the substrate or seek cover in the substrate. Given the high current velocities in the Cedar River, the only locations where fry could easily maintain their position in the current would be along the shore or on the bottom of the river channel. We were able to directly estimate the number of fry along the shoreline but not the number of fry along the bottom of the river channel. However, we were able to measure this number indirectly by examining predation by cottids in the midchannel area of a riffle at the I-405 site. Because of the high incidence of predation at this lighted site, we believe many sockeye salmon sought cover in the substrate and became vulnerable to predation by cottids. In all, we found 33 fry in 33 cottid stomach samples. Under similar conditions at a nearby control site, as well as at nine other sites further upstream with little lighting, only one salmonid fry was found in the stomachs of 109 cottids examined (Tabor, unpublished data). Similarly, in 2001, after the lights at the I-405 site were shielded, we observed no predation.

Predation of Fry

Under natural nighttime light intensity, sockeye salmon fry and cottids are probably spatially segregated because the fry occupy areas of faster water velocity (McDonald 1960), whereas cottids stay in close contact with the substrate and thus occupy areas with substantially slower water velocities. By selecting fast-flowing water areas, fry are able to move quickly downstream and reduce the likelihood of encounter with predators (Ginetz and Larkin 1976). Increased light causes fry to delay migration and to move to low-velocity water, where one would expect more frequent rates of encounter with cottids. Other research on predation of fry by cottids in the Cedar River has indicated that predation occurs primarily in low-velocity habitats such as pools and side channels (Tabor et al. 1998). Also, predation rates appear to be negatively related to streamflow. In addition, investigators have found that survival of juvenile salmonids is positively related to streamflow, which is probably related to reduced amounts of predation (Cada et al. 1997; Seiler and Kishimoto 1997)

Predation of fry by cottids appeared to be closely related to fry density at all field sites. As light intensity increased, the shoreline density of fry increased and subsequently the amount of predation increased. Cottids appeared to exhibit some type of functional response related to an increase in the abundance of fry. Because we conducted a variety of different field studies, it would be difficult to determine the exact type of functional response. Cottids may have a lesser ability to consume fry as light intensity increases, as demonstrated in the circular tank experiments, but the number of fry available to them at brighter light intensities will be substantially higher and thus overall predation should be greater, as was observed at field sites. Woodsworth (1982; prickly sculpin and sockeye salmon fry), Mace (1983; staghorn sculpin and chum salmon fry), and Jones (1986; prickly sculpin and chum salmon fry) studied the functional response of cottids feeding on salmonid fry. They all found that the functional response appeared to reach an asymptote at intermediate prey densities and then increase again at high prey densities. This may explain why we did not detect any differences in predation at Elliot Park. Jones (1986) also described a gorging behavior by prickly sculpin at high prey densities, wherein they would consume substantially more fry than the expected maximum ration. This may be similar to what we observed at high-light conditions at Lions Club Park, where fry were abundant and torrent sculpin of 90, 92, and 102 mm TL consumed 10, 13, and 12 fry, respectively.

Based on results from the artificial stream experiments and the Cedar River, increased light intensities greatly affect the behavior of sockeye salmon fry; however, the effect on predator behavior is not well understood. In field experiments, cottids appeared to exhibit a functional response in relation to an increase in the abundance of fry but did not exhibit any type of aggregative response (Sutherland 1996). However, our experiments were done over a short time and an aggregative response may take several days or weeks. In Lake Iliamna, Alaska, cottids exhibited a strong aggregative response in relation to the abundance of sockeye salmon eggs, but cottid movements to the salmon spawning sites took place over 3 weeks (Foote and Brown 1998). Therefore, cottids may exhibit an aggregative response to an increase in fry availability near permanent light structures. However, several alternative prey types exist in the Cedar River and cottids may not show a strong aggregative response such as that seen in Lake Iliamna, which is an oligotrophic system and perhaps limited in alternative prey. Jones (1986), in experimental studies with prickly sculpin, found that the abundance of alternative prey (amphipods and isopods) appeared to have almost as much influence as the abundance of the principal prey (chum salmon fry). In addition, cottids themselves may naturally avoid lighted areas because they too may become more vulnerable to predators. Movement into lighted areas may be a tradeoff for cottids, such that they have to balance increased risk of predation with increased prey availability.

Besides cottids, sockeye salmon fry in the Cedar River are also vulnerable to predation by salmonids, including rainbow trout (Beauchamp 1995), cutthroat trout, and juvenile coho salmon (Tabor et al. 1998). How increased light intensity affects predation of fry by salmonids is unclear. We used cottids for our laboratory experiments and field studies because they are an abundant predator in the Cedar River, are easy to collect, adjust readily to laboratory conditions, and are not as mobile as salmonids. Because salmonid predators are primarily visual predators, the effect of light intensity may be more pronounced when salmonids are present. Unlike cottids, salmonids may forage more effectively at higher light intensities. Predation of sockeye salmon fry by rainbow trout in artificial streams increased with increasing light intensity at intensities of less than 0.1 lx (Ginetz and Larkin 1976). Alternatively, salmonids are typically nocturnal during this time of the year (Riehle and Griffith 1993; Contor and Griffith 1995) and thus may avoid lighted areas. Additional field sampling needs to be undertaken to understand how increased light intensity would change the predation rate of fry by salmonid predators.

Tank and artificial stream experiments produced contrasting results. Tank experiments indicated that predation of sockeye salmon fry increased as light intensities decreased, whereas artificial stream experiments indicated the opposite. The reason for this large discrepancy is probably differences in current velocities. The artificial stream experiments were done in a flow-through system with strong current velocities (midchannel surface velocities ranging from 0.37 to 0.12 m/s), which created a fast-water refuge from cottids. In contrast, the tank experiments were done with little flow and no opportunity for the fry to emigrate downstream. In the tank experiments, predator and prey both occupied the same habitat and the reduction in predation with increased lighting probably reflects both the foraging ability of the sculpin and the ability of the fry to avoid them. The circular tank experiment made clear that both prickly sculpin and torrent sculpin can be highly effective predators in complete or near-complete darkness and that increased ambient light does not necessarily enhance their ability to prey on sockeye salmon fry. Hoekstra and Janssen (1985) demonstrated that blinded mottled sculpin *C. bairdi* were able to feed on mobile prey just by using their lateral line system.

In contrast to our results, Ginetz and Larkin (1976) found that predation of sockeye salmon fry by rainbow trout in artificial streams decreased as light intensity increased from 0.5 to 3.0 lx. Discrepancies between their experiments and this study are probably attributable to the predators used, the current velocities, and the size of the artificial stream. Ginetz and Larkin (1976) used a 0.6-m-wide experimental stream and rainbow trout, a highly mobile predator. Our experimental stream was 1.5 m wide and the predator we used was prickly sculpin, a substantially less mobile species. The current velocities used by Ginetz and Larkin were 0.12 m/s, which means there was probably no location where rainbow trout could not forage effectively. McDonald (1960) found that most sockeye salmon fry migrate in current velocities greater than 0.65 m/s, which may be too high for rainbow trout and other predators to forage effectively. Other researchers have also conducted light experiments with juvenile salmonids in which there is little or no current velocity (Patten 1971; Mace 1983; Petersen and Gadomski 1994). Their results may not apply to emigrating fish in natural situations if high current velocities are available. In those controlled experiments, predators usually had easy access to prey and the experiments may not have adequately simulated natural conditions, where high current velocities are available that create a fast-water refuge. In our artificial stream, current velocities were probably high enough to create such a refuge from prickly sculpin.

The size of the experimental field units (8 m shoreline length) appeared to work well for detecting differences in fry abundance but may have been too small for estimating predation rates. We could detect differences in predation between lighted areas and control areas at Lions Club Park, but we were often unable to detect differences in results between different light intensities. In some experimental units few predators were collected. Also, the diets of cottids can vary between individual fish; even when fry are abundant, many cottids will not consume them, and each site will include a variety of other prey types such as aquatic insects or oligochaetes. If many of the male cottids are guarding egg nests, they may not be actively searching for prey. In mottled sculpin, the male may spend 8 weeks fanning and protecting eggs and young (Downhower and Brown 1980). In most areas, a 20–30 m shoreline would probably be adequate to collect enough cottids to get an accurate estimate of predation. Additionally, had we extended the experiments—which lasted for only a few hours—over the entire night we may have seen more predation and thus been better able to detect differences between treatments.

Experiments at the Lions Club Park demonstrated that shoreline habitat type can have an important effect on the number of sockeye salmon fry delayed in their emigration and the subsequent predation that ensues. This effect was probably in large part attributable to water velocities as well as substrate type. Light caused sockeye salmon fry to move to low-velocity areas. The riprap banks were steeper and had a narrower area of low-velocity water than did the gravel shoreline. The two habitat types may also have had differences in predator abundance, which could influence the number of sockeye salmon fry. The results of our laboratory experiments and other studies (Ginetz and Larkin 1976; Gaudin and Caillere 1985; Bardonnet and Heland 1994) have demonstrated that the presence of predators increases the downstream movement of salmonid fry. Typically, large cottids are more numerous in larger substrates such as riprap than in smaller substrates (Tabor et al. 1998). The abundance of other predators such as rainbow trout may also be greater near a riprap bank (Lister et al. 1995).

The substrate type across the channel width may also have an important effect on predation in a lighted area. Larger substrates will create a rougher river channel and may have more abundant low-velocity locations for sockeye salmon fry. However, these same sites will probably also have more large cottids. In riffles of the Cedar River, the abundance of cottids larger than 50 mm TL was greatest in areas with large substrates such as cobble (Tabor et al. 1998). At the I-405 bridge site, the substrate consisted primarily of cobble and large gravel; there we were able to collect several cottids larger than 50 mm TL. At another lighted bridge site in the Cedar River, however, the substrate was mostly small gravel, and few cottids larger than 50 mm TL were collected; thus, the overall predation at that site was probably minimal (Tabor, unpublished data).

Management Implications

In the lower Cedar River, nighttime lighting appears to come from three major sources: direct artificial lighting, the moon, and reflected lighting off of clouds. Direct lighting is intense lighting that occurs in a relatively small area every night and usually all night. In contrast, reflected light and moonlight are not very intense but they are spread over a much larger area and vary greatly with the weather and moon phase. Direct lighting probably has strong localized effects on sockeye salmon fry, whereas reflected lighting and moonlight probably have weak effects over a large area. Which of these has more overall effect on sockeye salmon fry is difficult to assess. However, it is much easier to reduce direct lighting than to address reducing reflected light. Direct lighting can be turned off, redirected, or shielded. Reducing reflected light would be a much larger and far more difficult management objective.

Overall, our results suggest that reductions in light intensity can be beneficial for emigrating sockeye salmon fry and that the impact of lighting should be considered for any future development project. For example, by reducing the lighting at the I-405 bridge site, we substantially reduced predation on sockeye salmon fry. Attempting to keep light values below 0.1 lx appears to be a prudent management goal.

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